Geographical Ecology of the Butterfly Fauna of the Krakatau Islands, Indonesia*

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Abstract The Krakatau Islands, consisting of 4 islets, are situated in the Sunda Strait between Java and Sumatra in Indonesia. As is well known, the islands were almost certainly completely sterilized by the world-famous big eruption in 1883. In association with the international research program on "100 years development of Krakatau and its surroundings" organized by the Indonesian Institute of Sciences (LIPI), the author visited there in 1982 to study the insect fauna of the islands. A total of 39 butterfly species were collected on the Krakataus, 29 on Panaitan Island and 18 at Carita, a small village along the west coast of Java. In the light of recent biogeographical theories, the faunistic features and recolonization of the Krakataus by butterflies are discussed, based on the collecting records of the present and previous surveys together with floral lists compiled by plant ecologists.

Introduction

The Krakatau Islands now consist of 4 islets, namely, Rakata Besar (or Rakata), Rakata Kecil (or Panjang), Sertung and Anak Krakatau, situated in the Sunda Strait between Java and Sumatra, Indonesia (Fig. 1). The Krakataus were, however, previously composed of 3 islets, Krakatau (now called Rakata Besar), Lang (Rakata Kecil) and Verlaten (Sertung). As is well known, on 27 August 1883, volcanic activities of 3 vents on Krakatau gave rise to the world-famous eruption which completely destroyed the northern 2/3 of the island. The remaining 1/3 of Krakatau, and its 2 neighbouring islands, Rakata Kecil and Sertung, were almost certainly completely sterilized by a thick layer of hot ash and pumice (DOCTERS VAN LEEUWEN, 1936; RICHARDS, 1952). In 1927–1930, submarine activities created a new volcanic island, Anak Krakatau in the centre of the above-mentioned 3 islands. Thus, the Krakataus have a relatively short (50–100 years) historical background of ecological succession.

In association with the international research program on "100 years development of Krakatau and its surroundings" organized by the Indonesian Institute of Sciences (LIPI), 2 Japanese expedition teams visited there to study the ecological succession and the formation process of volcanic ash soil. Mr. Sk. YAMANE (Kagoshima Univ., first expedition team) and the present author (second one) had an opportunity to collect insects on the islands in July–August and October–November 1982, respectively. In order to compare the insect fauna of the Krakataus with that of the surroundings, the

* This study was supported by Grant-in-Aid Nos. 57041044 and 58043044 from the Ministry of Education, Science and Culture, Japan, and also by a grant from the Toyota Foundation, No. 81-1-242.

蝶と蛾 *Tyô to Ga*, **35** (2): 47–74, 1984

present author collected insects also at Carita, a small village along the west coast of Java and on Panaitan Island (Fig. 1) from which there are a few previous collecting records of butterflies (ACKERY & VANE-WRIGHT, 1984).

The insect fauna of the Krakatau Islands was surveyed chiefly by JACOBSON (1909), DOCTERS VAN LEEUWEN (1920, 1922) and DAMMERMAN (1922, 1928, 1929, 1948), and occasionally by others. Of butterflies, 42 species were listed in DAMMERMAN (1948). The Zoological Museum in Bogor sent an expedition team to the islands in 1955, but the result has not yet been published. Unfortunately, no extensive faunistic survey was performed on the islands thereafter until 1982.

This paper records the butterflies which were collected from the Krakataus and the surroundings almost 100 years after the eruption of 1883. Based on the collecting records of the present and previous surveys, the faunistic features and recolonization of the Krakataus by butterflies are also discussed in the light of recent biogeographical theories presented by MACARTHUR & WILSON (1967), DIAMOND & MAY (1976) and others.

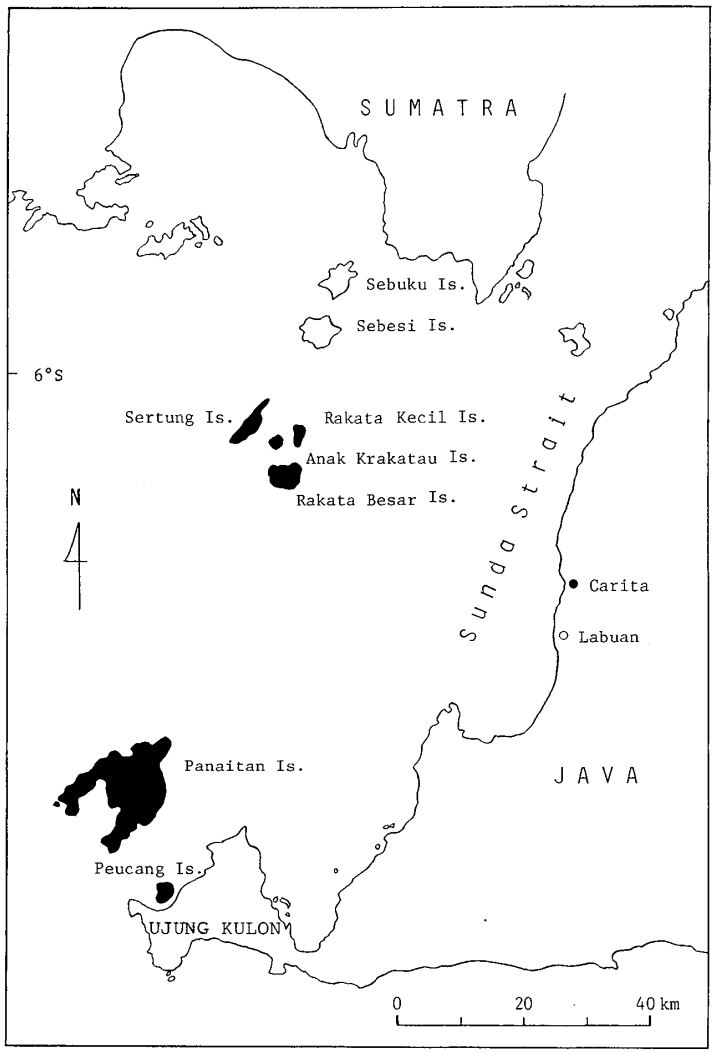

Fig. 1. Map of the Krakatau Islands and surroundings.

Survey Areas

1. *Topography and vegetation*

The Krakatau Islands other than Anak Krakatau are covered by a thick layer of white volcanic ash which was produced by the 1883 eruption. The ash layer has been eroded by the surface flow of rain since 1883 to make deep gullies on the slopes and a secondary deposit on the shore (TAGAWA *et al.*, in press). Rakata Besar (1,152 ha) is the largest island with the most diversified topography of the island group and a highest point of 730 m (see Sk. YAMANE, 1983). It is mainly covered by forest of *Neonauclea calycina*. Undergrowth in the forest is characterized by *Ficus* spp., *Leea sambucina*, *Leucosyke capitellata* and *Villebrunea rubescens*. Both Sertung (784 ha) and Rakata Kecil (272 ha) are generally flat and there are no prominent peaks but gentle hills lower than 182 m. The following plants are dominant in various habitats on the two islands: *Casuarina equisetifolia*, *Dysoxylum caulostachyum*, *Ficus* spp., *Terminalia catappa* and *Timonius compressicaulis*. Anak Krakatau (280 ha) has a highest point of 181 m on the central cone. At least 90% of the island may be barren due to continuous volcanic activity. The vegetation on the island is represented chiefly by *Casuarina equisetifolia*, *Ipomoea pes-caprae* and *Saccharum spontaneum*, which grow in restricted areas near the beach.

Panaitan Island (at least 9,000 ha) is about 10 km from Ujung Kulon Nature Reserve, the westernmost peninsular of Java. The island, as well as the penisular, has been protected from human activities and is thought to have been less influenced by the 1883 eruption than the Krakataus. Therefore, the island has a typical tropical seasonal forest, together with a number of wetland vegetation types such as mangrove and swamp forest (TAGAWA *et al.*, in preparing).

Carita is a small village along the west coast of Java and is characterized by the presence of open grasslands, rice fields, bushes of *Hibiscus* and plantations of coconut palms and broad-leaved trees.

2. *Climate*

According to the only available climatological data from the Krakatau Islands seen by STEHN in 1929 (VAN BAREN, 1931), the dry season begins in May and ends in October, and a total of 2,620 mm rainfall is recorded during the year. The temperature is almost constant, and monthly mean temperature vary from 26.9°C (July, December) to 28.7°C (October). The west monsoon brings heavy rain from the Indian Ocean and the east monsoon brings dry air from Australia.

Methods

1. *Methods*

Butterflies were collected mainly in the daytime with an insect net on flowers, in

bushes on the beach, in gaps in the forest, around forest edges and inside forests of various trees. Some satyrids were caught in the evening around the tent sites on Rakata Besar and Sertung. Table 1 shows the net duration of time devoted by the present author and Mr. Sk. YAMANE to the collection of insects in each locality. Sk. YAMANE spent 19 days on the Krakatau Islands in July and August 1982. The present author collected for 3 days on each of Panaitan Island and Carita (Fig. 1), and for 16 days on the Krakataus.

Table 1. Duration of days devoted to collection of insects including butterflies at each locality in the 1982 surveys.

Collector(s)	Season	Carita W. Java	Panaitan	Rakata Besar	Rakata Kecil	Sertung	Anak Krakatau
Sk. YAMANE*	July, Aug.	—	—	7	3	6	3
J. YUKAWA & E. SUZUKI**	Oct., Nov.	3	3	5	3	6	2
Total		3	3	12	6	12	5

* Sk. YAMANE visited Carita, but no butterflies were collected.
** About 30 individuals of butterflies were caught by E. SUZUKI.

2. *Host plant information*

Information concerning host plants and distribution ranges of the Javanese and Sumatran butterflies were chiefly based on the following references: BELL (1912–1914), CORBET & PENDLEBURY (1978), EVANS (1949), FRUHSTORFER (1911–1926), FUKUDA (1974), HILL *et al.* (1978), KAWAZOÉ & WAKABAYASHI (1976), KERSHAW (1907), PIEPERS & SNELLEN (1913), TSUKADA & NISHIYAMA (1980), YATA & MORISHITA (1981) and AOKI *et al.* (1982).

Collecting records of plant species on the islands were related to the results of floral surveys carried out in 1979 by the Hull University team (FLENLEY & RICHARDS, 1982; WHITTAKER *et al.*, 1984) and in 1982 by the Kagoshima University team (TAGAWA *et al.*, in press; TAGAWA & SUZUKI, unpublished).

3. *Some difficulties in comparing different surveys*

Butterflies can more easily be identified, frequently at the subspecies level and sometimes even in the air, than other insect groups. Their host plants and distributional range are also relatively well known. In addition they are sighted more frequently during surveys owing to their colourful wing pattern, particularly in the tropics. Thus butterflies provide faunistic data in a relatively convenient way. However, there are difficulties in comparing faunistic data between two or more surveys.

One of the main difficulties is to evaluate the intensity of the surveys. The intensity is determined by such factors as the number of collectors, their skill and experience, the total time devoted to collection, and the weather. Another difficulty is the reliance to be placed on absences. A species may be erroneously recorded as absent when collecting has been insufficient or at the wrong season, or when a species is rare.

Table 2. List of butterflies collected or observed in 1982 on Panaitan and the Krakatau Islands.

Family	Species	Panaitan	Rakata Besar	Rakata Kecil	Sertung	Anak Krakatau
PAPILIONIDAE	*Graphium agamemnon agamemnon* (L.)	●	— — — ○	— — — ○	— — — —	— —
	Graphium doson evemonides (HONRATH)	●	— — — —	— — — —	— — — —	— —
	Pachliopta aristolochiae adamas (ZINKEN)	—	— ▲ ■ ●	— — — —	— — — ●	— —
	Pachliopta aristolochiae antiphus (FAB.)	—	— ▲ ■ ●	— — — —	— — ■ ●	— —
	Papilio helenus engarius DOHERTY	●	— — — —	— — — —	— — — —	— —
	Papilio peranthus FAB.	●	— — — —	— — — —	— — — —	— —
	Troides helena helena (L.)	—	▼ ▲ ■ ●	— — — ○	— — ■ ●	— —
PIERIDAE	*Appias indra leptis* (FELDER)	●	— — — —	— — — —	— — — —	— —
	Appias lyncida lyncida (CRAMER)	●	— — — —	— — — —	— — — —	— —
	Appias nero nero (FAB.)	●	— — — —	— — — —	— — — —	— —
	Appias paulina leis (HÜBNER)	●	— — — —	— — — —	— — — —	— —
	Belenois java java (SPARRMAN)[1]	—	— ▲ — —	— — — ●	— — — —	— —
	Catopsilia pomona pomona (FAB.)[2]	○	— — ■ ○	— — — —	— — — ○	— —
	Cepora iudith iudith (FAB.)	●	— — — —	— — — —	— — — —	— —
	Eurema alitha sankapura (FRUH.)	—	— — — ●	— — — —	— — — —	— —
	Eurema blanda blanda (BOISD.)	●	— ▲ ■ ●	— — — ●	— ▲ ■ ●	— —
	Eurema hecabe hecabe (L.)[3]	—	— — ■ —	— — — —	— ▲ ■ ●	— —
	Gandaca harina harina (HORSFIELD)	●	— — — —	— — — —	— — — —	— —
	Pareronia valeria leona (FRUH.)	●	— — — —	— — — —	— — — —	— —
DANAIDAE	*Danaus chrysippus bataviana* MOORE	—	— — — —	— — — —	— ▲ — ○	— —
	Danaus genuita intensa MOORE[4]	—	▼ ▲ ■ —	— — ■ —	— ▲ ■ ●	— —
	Danaus genuita sumatrana MOORE[5]	—	— — ■ —	— — — —	— — ■ —	— —
	Danaus melanippus melanippus (CRAMER)	—	▼ ▲ ■ —	— — ■ —	— — ■ —	— —
	Euploea crameri LUCAS	●	— — — —	— — — —	— — — —	— —
	Euploea modesta BUTLER	●	— — — —	— — — —	— — — —	— —
	Euploea sp.	—	— — — ○	— — — —	— — — ○	— —
	Radena juventa (CRAMER)	—	— ▲ ■ ●	— — — ●	— ▲ ■ ●	— —

Table 2. (*continued*)

Family	Species	Panaitan	Rakata Besar	Rakata Kecil	Sertung	Anak Krakatau
SATYRIDAE	*Melanitis leda* (L.)	—	— — ■ ●	— — — ●	— — — ●	— ●
	Mycalesis horsfieldii horsfieldii (MOORE)	—	— ▲ ■ —	— — — —	— — ■ ●	— —
	Mycalesis janardana janardana MOORE	—	— ▲ — ●	— — — —	— — ■ ●	— —
	Orsotriaena medus (FAB.)	—	— ▲ ■ —	— — ■ —	— — — —	— —
	Ypthima horsfieldii MOORE	—	— ▲ ■ ●	— — — —	— ▲ ■ —	— —
	Ypthima philomela philomela (L.)	—	— ▲ — —	— — — —	— — — —	— —
NYMPHALIDAE	*Cethosia hypsea* DBL.	●	— — — —	— — — —	— — — —	— —
	Charaxes sp.	●	— — — —	— — — —	— — — —	— —
	Chersonesia rahria (MOORE)	●	— ▲ — —	— — — ●	— — — —	— —
	Cirrochroa tyche C. & R. FELDER	●	— — ■ —	— — — —	— — — —	— —
	Euthalia mahadeva (MOORE)	●	— — — —	— — — —	— — — —	— —
	Hypolimnas anomala (WALLACE)	—	— ▲ ■ ●	— — — ●	— ▲ ■ ●	— ●
	Hypolimnus bolina bolina (L.)	—	— ▲ ■ ●	— — — —	— — ■ ●	— —
	Moduza procris minoe FRHST.	—	— — — —	— — — —	— ▲ — —	— —
	Neptis hylas (L.)	○	▼ ▲ ■ ○	— — — —	— — — ●	— —
	Phalanta phalantha (DRURY)	—	— — — —	▽ — — —	— — — —	— —
LYCAENIDAE	*Allotinus felderi* SEMPER	—	— — — —	— — — —	— — — ●	— —
	Arhopala pseudocentaurus pseudocentaurus (DBL.)[6]	—	— ▲ ■ —	— — — ●	— — ■ ●	— —
	Catochrysops panormus (C. FELDER)	●	— — ■ —	— — — —	— — — —	— —
	Catochrysops strabo (FAB.)	—	— — — ●	— — — —	— — ■ ●	— ●
	Catopylops ancyra (C. FELDER)[7]	—	— ▲ — —	— — — —	— — — —	— —
	Deudorix jarbas dekaiarchus FRHST.	—	— ▲ — —	— — — —	— — — —	— —
	Euchrysops cnejus cnejus (FAB.)	—	— ▲ ■ —	— — — —	— ▲ ■ ●	— —
	Hypolycaena erylus erylus (GODART)	—	— — — ●	— — — ●	— ▲ — ●	— —
	Jamides aratus (STOLL)	—	— — — ●	— — — —	— — — —	— —
	Jamides bochus (STOLL)	●	— ▲ ■ —	— — — —	— — — ●	— —
	Jamides celeno (CRAMER)[8]	—	— ▲ ■ ●	— — — ●	— ▲ ■ ●	— ●
	Jamides elpis (GODART)	●	— — — —	— — — —	— — — —	— —
	Jamides malaccanus (RÖBER)	●	— — — —	— — — —	— — — —	— —

Table 2. (*continued*)

Family	Species	Panaitan	Rakata Besar	Rakata Kecil	Sertung	Anak Krakatau
LYCAENIDAE	*Lampides boeticus* (L.)[9]	—	— — ■ —	— — — ●	— — ■ —	— ●
	Loxura atymnus (STOLL)	—	— — ■ —	— — — —	— — — —	— —
	Megisba malaya malaya (HORSFIELD)	—	— — — ●	— — — —	— — — —	— —
	Miletus symethus (CRAMER)	—	— — — ●	— — — —	— — — —	— —
	Miletus sp.	●	— — — —	— — — —	— — — —	— —
	? *Nacaduba pactolus* (C. FELDER)	●	— — — —	— — — —	— — — —	— —
	Petrelaea dana dana (de NICÉVILLE)	—	— — — ●	— — — —	— — — —	— —
	Prosotas dubiosa (SEMPER)	●	— — — —	— — — ●	— — — —	— —
	Prosotas lutea (MARTIN)	—	— — — —	— — — —	— — — ●	— —
	Zizina otis lysizone (SNELLEN)	—	— — — —	— — — —	— — — ●	— ●
	Zizula hylax (FAB.)	—	— — — —	— — — —	— — — ●	— —
HESPERIIDAE	? *Borbo cinnara* (WALLACE)	—	— — — —	— — — —	— — — ●	— ●
	Notocrypta sp.	—	— ▲ — —	— — — —	— — — —	— —
	? *Pelopidas agna* (MOORE)	—	— — — —	— — — —	— — — ●	— —
	Pelopidas conjunctus (HERRICH-SCHÄFFER)	—	— ▲ ■ —	— — — —	— ▲ — —	— —
	Pelopidas mathias (FAB.)	—	— ▲ ■ —	— — ■ —	— — — —	— —
	Polytremis lubricans (HERRICH-SCHÄFFER)[10]	—	▼ ▲ — —	— — — —	— — — —	— —
	Potanthus confucius (C. & R. FELDER)[11]	●	— ▲ ■ ●	— — ■ ●	— ▲ ■ ●	— ●
	Tagiades sp.	—	— — — —	— — — —	— — ■ —	— —
	Telicota augias (L.)	—	— ▲ — —	— — — —	— — — —	— —

▼: collection records by JACOBSON in 1908 (JACOBSON, 1909). ▽: observation by JACOBSON in 1908 (JACOBSON, 1909). ▲: collection records mainly by DAMMERMAN from 1919 to 1922 and partly by LEEFMAN in 1919 (DAMMERMAN, 1922, 1929). ■: collection records by DOCTERS VAN LEEUWEN in 1928 and 1932 and by DAMMERMAN from 1932 to 1934 (DAMMERMAN, 1948). ●: collection records by YUKAWA and Sk. YAMANE in 1982 (YUKAWA, present paper). ○: observation by YUKAWA in 1982 (YUKAWA, present paper).

Some of the scientific names quated in DAMMERMAN (1948) are replaced by new ones, among which those changed largely are numbered and refer to the following old names, respectively:

1)=*Anaphaeis java coronea* CR., 2)=*Catopsilia crocale* CR., 3)=*Terias hecabe sankapura* FRHST., 4)=*Danais plexippus intensa* MR., 5) =*Danais plexippus sumatrana* MR., 6)=*Amblypodia centaurus pseudocentaurus* DBL., 7)=*Nacaduba ancyra* FELDER, 8)=*Lampides celeno ruvana* FRHST., 9)=*Cosmolyce baetica* L., 10)=*Parnara toona* MR., 11)=*Padraona dara* KOLL.

In order to overcome one of these difficulties, Sk. YAMANE (1st expedition team) attempted to compare the net duration of time devoted to collecting in the present and the previous 3 major surveys: in 1908 by JACOBSON (1909), in 1919–1922 by DAMMERMAN (1922, 1929) and in 1932–1934 by DAMMERMAN (1948). He concluded that such differences between surveys were relatively trivial (Sk. YAMANE, 1983).

The present author assessed the reliability of absence records of certain butterfly species from the Krakataus by confirming the absence of their known host plants and of related plant species, based on the more extensive data on the recent flora and vegetation on the islands (FLENLEY & RICHARDS, 1982; TAGAWA & SUZUKI, unpublished). Possible omission of certain plant species is inevitable but seems to have been considerably minimized because of the relatively frequent and intensive surveys by botanists (FLENLEY & RICHARDS, 1982). The failure to record butterfly species because of seasonal changes in occurrence might partly be overcome by visiting the islands on 2 different occasions in 1982.

Results and Discussion

1. *General notes*

A total of 60 butterfly species were collected or observed in 1982 on the Krakatau Islands and Panaitan Island (Fig. 1; Table 2). Of these, 29 species were found on Panaitan, and 39 on all the Krakatau Islands taken together. On the Krakataus, Rakata Besar had 22 species, Rakata Kecil 14, Sertung 28 and Anak Krakatau only 8 (Table 3). No butterfly species was previously collected on Anak Krakatau. Only 10 out of the 29 species collected on Panaitan were also collected on the Krakataus (Table 2).

Eighteen species were collected at Carita (Table 4). Only half of these were found also on the Krakataus. It should be remarked here that at Carita many males and females of *Catopsilia pomona pomona* were observed migrating from the southeast to the northwest on the morning of 16 and 17 November 1982 (YUKAWA, 1983). On the Krakataus, however, no migratory trend was observed for this species. In addition, *Catopsilia pyranthe*, *Delias hyparete hyparete* and *Junonia atlites* were commonly observed in the village of Carita near the seashore, but they were neither collected nor observed on the Krakataus. Thus, the species composition on the Krakataus is somewhat different from that on Panaitan or at Carita, lacking many species which are thought to occur abundantly in West Java.

Insects which invade new habitats sometimes increase their numbers and reach an outbreak situation, the phenomenon being frequently encountered in populations established on islands (ELTON, 1958). On the Krakataus, DAMMERMAN (1948) noted the sudden appearance of large numbers of 2 species of skinks, *Mabuya multifasciata* and *Lygosoma atrocostatum* during his surveys in the 1920s and 1930s. Outbreaks were also found in the 1982 surveys of such organisms as a scale insect, *Crypticerya jacobsoni* (YUKAWA, 1984), a fruit fly, *Dacus albistrigatus* (YUKAWA, 1984) and 2 species of rats, *Rattus rattus* and *Rattus tiomanicus* (IWAMOTO, in preparing). However,

Table 3. Number of butterfly species found on the Krakataus and on Panaitan during different collection periods.

	Rakata Besar				Rakata Kecil				Sertung				Anak Krakatau		All the Krakataus				Panaitan
	▼	▲	■	●	▼	▲	■	●	▼	▲	■	●	■	●	▼	▲	■	●	●
PAPILIONIDAE	1	2	2	3	0	0	0	2	0	0	2	2	0	0	1	2	2	3	4
PIERIDAE	0	2	3	3	0	0	0	2	0	2	2	3	0	0	0	3	3	5	9
DANAIDAE	2	3	3	2	0	0	2	1	0	3	3	4	0	0	2	4	3	4	2
SATYRIDAE	0	5	4	3	0	0	1	1	0	1	3	3	0	1	0	5	5	4	0
NYMPHALIDAE	1	4	4	3	1	0	0	2	0	2	2	3	0	1	2	5	4	4	6
LYCAENIDAE	0	6	7	7	0	0	0	5	0	3	5	10	0	4	0	7	8	16	7
HESPERIIDAE	1	6	3	1	0	0	2	1	0	2	2	3	0	2	1	6	4	3	1
TOTAL	5	28	26	22	1	0	5	14	0	13	19	28	0	8	6	32	29	39	29

▼: collection records by JACOBSON in 1908 (JACOBSON, 1909). ▲: collection records mainly by DAMMERMAN from 1919 to 1922 and partly by LEEFMAN in 1919 (DAMMERMAN, 1922, 1929). ■: collection records by DOCTERS VAN LEEUWEN in 1928 and by DAMMERMAN from 1932 to 1934 (DAMMERMAN, 1948). ●: collection records by YUKAWA and Sk. YAMANE in 1982 (YUKAWA, present paper).

Table 4. A list of butterflies collected at Carita, and their collection records on the Krakataus.

Family	Species	Collection records on the Krakataus*
PAPILIONIDAE	*Losaria coon coon* (FAB.)	none
PIERIDAE	*Appias nero nero* (FAB.)	none
	Catopsilia pomona pomona (FAB.)	RB, S
	Catopsilia pyranthe pyranthe (L.)	none
	Delias hyparete hyparete (L.)	none
	Eurema alitha sankapura (FRUH.)	RB, S
	Eurema hecabe hecabe (L.)	S
DANAIDAE	*Euploea modesta* BUTLER	none
	Euploea mulciber basilissa CRAMER	none
	Radena juventa (CRAMER)	RB, RK, S
SATYRIDAE	*Amathusia* sp.	none
	Elymnias sp.	none
	Ypthima horsfieldii MOORE	RB, S
NYMPHALIDAE	*Junonia atlites* L.	none
	Neptis hylas (L.)	RB, S
LYCAENIDAE	*Arphopala pseudocentaurus pseudocentaurus* (DBL.)	RK, S
	Jamides celeno (CRAMER)	AK, RB, RK, S
	Zizina otis lysizone (SNELLEN)	AK, S

* AK: Anak Krakatau, RB: Rakata Besar, RK: Rakata Kecil, S: Sertung, see Table 2 for further details of the collection records on the Krakataus.

no evidence of outbreaks of butterfly species on the Krakataus has been observed.

2. *Derivation of the fauna*

For 28 of the 60 speices collected on the Krakataus and Panaitan, butterflies could be identified at subspecies level (Tables 2, 5 & 6). They chiefly concerned the families Papilionidae and Pieridae, and in part the Danaidae, Satyridae, Nymphalidae and Lycaenidae. Subspecies identifications were not possible for the hesperiid species. The identified subspecies were divided into 3 categories: Javanese, Sumatran and Java-Sumatran subspecies. The category Java-Sumatran includes species distributed in both Java and Sumatra, and thus the natural range could not be determined, as well as the hesperiids and other butterflies which could not be identified at subspecies level. However, the derivation of faunas can be indicated by the relative abundance of subspecies in the Javanese and Sumatran categories.

Eight of 12 subspecies on Panaitan were representatives of Javanese ones which are not distributed in Sumatra, and the remaining 4 belonged to subspecies found on both Java and Sumatra (Table 5). There were no exclusively Sumatran subspecies on Panaitan. It is to be expected that a large majority of the known subspecies on Panaitan should be exclusively Javanese subspecies since the island is only about 10 km from Ujung Kulon, the westernmost peninsular of Java (Fig. 1). Therefore, the butterfly

Table 5. Relative abundance of Javanese, Sumatran and Java-Sumatran subspecies among the butterflies collected on Panaitan in 1982.

Family	Species	Javanese subspecies	Sumatran subspecies	Java-Sumatran subspecies
PAPILIONIDAE	*Graphium agamemnon agamemnon*	—	—	●
	Graphium doson evomonides	—	—	●
	Papilio helenus engarius	—	—	●
PIERIDAE	*Appias indra leptis*	●	—	—
	Appias lyncida lyncida	●	—	—
	Appias nero nero	●	—	—
	Appias paulina iles	●	—	—
	Catopsilia pomona pomona	—	—	●
	Cepora iudith iudith	●	—	—
	Eurema blanda blanda	●	—	—
	Gandaca harina harina	●	—	—
	Pareronia valeria leona	●	—	—
	Total number (%)	8 (66.7)	0 (0)	4 (33.3)

Table 6. Relative abundance of Javanese, Sumatran and Java-Sumatran subspecies among the butterflies collected on the Krakataus in 1982.

Family	Species	Javanese subspecies	Sumatran subspecies	Java-Sumatran subspecies
PAPILIONIDAE	*Graphium agamemnon agamemnon*	—	—	●
	Pachliopta aristolochiae adamas	●	—	—
	Pachliopta aristolochiae antiphus	—	●	—
	Troides helena helena	—	—	●
PIERIDAE	*Belenois java java*	●	—	—
	Catopsilia pomona pomona	—	—	●
	Eurema alitha sankapura	●	—	—
	Eurema blanda blanda	●	—	—
	Eurema hecabe hecabe	—	—	●
DANAIDAE	*Danaus chrysippus bataviana*	●	—	—
	Danaus genuita intensa	●	—	—
SATYRIDAE	*Mycalesis horsfieldii horsfieldii*	●	—	—
	Mycalesis janardana janardana	●	—	—
NYMPHALIDAE	*Hypolimnas bolina bolina*	—	—	●
LYCAENIDAE	*Arhopala pseudocentaurus pseudocentaurus*	—	—	●
	Euchrysops cnejus cnejus	—	—	●
	Hypolycaena erylus erylus	—	—	●
	Megisba malaya malaya	●	—	—
	Petrelaea dana dana	—	—	●
	Zizina otis lysizone	—	—	●
	Total number (%)	9 (45.0)	1 (5.0)	10 (50.0)

species collected on Panaitan, although few, are considered to represent a part of the butterfly fauna of the tropical seasonal (monsoon) forest of West Java.

On the Krakataus, which are about 40 and 35 km distant from Java and Sumatra, respectively, Javanese subspecies were distinctly more abundant than Sumatran ones (Table 6). This suggests the possibility that a large majority of butterflies on the Krakataus are derived from Java rather than from Sumatra. A similar tendency was also noted for aculeate Hymenoptera (Sk. YAMANE, 1983).

DAMMERMAN (1948) considered that the majority of Krakatau species were of Sumatran origin, basing his conclusion largely on an analysis of the avifauna. He noted that some species of birds that were not found on Rakata Besar were observed on Rakata Kecil and Sertung, which are situated nearer to Sumatra. In contrast to this conclusion, the insect fauna of the Krakataus as represented by butterflies and aculeate Hymenoptera consists largely of species of Javanese origin, in spite of the fact that there are two possible "stepping stone islands" (MACARTHUR & Wilson, 1967), Sebuku and Sebesi between Sumatra and the Krakataus and no such islands between Java and the Krakataus.

3. *Coexistence of two subspecies*

There are 2 examples of a Javanese subspecies coexisting on the Krakataus with a Sumatran subspecies of the same species. *Pachliopta aristolochiae adamas* is a Javanese subspecies, being characterized by having white spots on hind wings (Fig. 2A). *P. aristolochiae antiphus* is a Sumatran subspecies, lacking the white spots (Fig. 2B). These 2 subspecies have been known to coexist since 1919 on Rakata Besar (DAMMERMAN, 1922, 1948). Their coexistence on Sertung was observed by the 1982 surveys and reconfirmed on Rakata Besar. However, no intermediates were obtained. These observations suggest that a mechanism of reproductive isolation might have already become established between the 2 subspecies. Another example of such coexistence has been noted on Rakata Besar and Sertung for the 2 subspecies, *intensa* and *sumatrana* of *Danaus genuita* (DAMMERMAN, 1948).

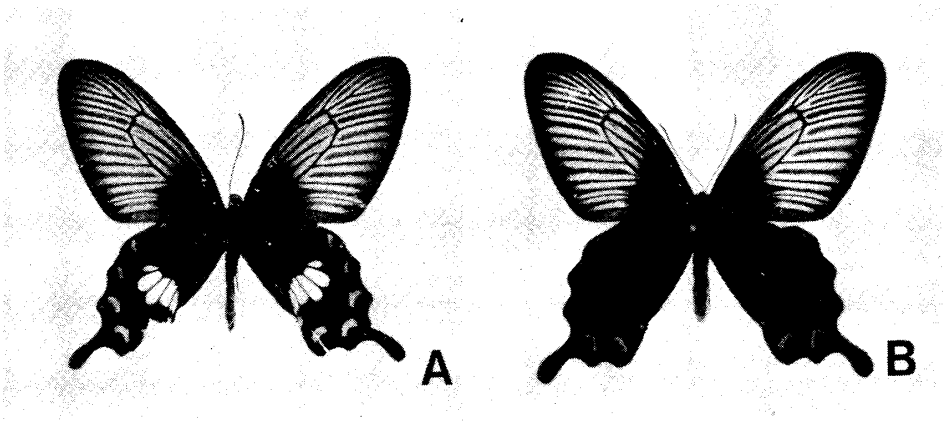

Fig. 2. A: *Pachliopta aristolochiae adamas* (♀), Javanese subspecies; collected on Sertung, 14. Nov. 1982, J. YUKAWA leg. B: *P. aristolochiae antiphus* (♀), Sumatran subspecies; collected on Rakata Besar, 29. Oct. 1982, J. YUKAWA leg.

4. *Area-species relation*

MacArthur & Wilson (1976) pointed out that the number of species on a given island is usually approximately related to the area of the island. The number of butterfly species found on the Krakatau Islands in 1982 varied from 8 to 28 (Table 3). The 2 larger islands, Rakata Besar (1,152 ha) and Sertung (784 ha) have more species than the smaller ones, Rakata Kecil (272 ha) and Anak Krakatau (280 ha). However, the correlation with area was not exact. The unusually rich fauna of Sertung may be due to the presence of more advanced forest, dominated by *Dysoxylum caulostachyum* and its associated undergrowth, which was relatively rare on Rakata Besar (Tagawa *et al.*, in press).

The species number was low on the active volcanic island, Anak Krakatau, which has undergone only 50 years of ecological succession since its emergence above sea level. The markedly poor vegetation, consisting of at most 50 vascular plant species (Flenley & Richards, 1982; Tagawa & Suzuki, unpublished), and the limited substrate suitable for plant growth, apparently account for the unexpectedly low species number of such phytophagous insects as butterflies on that island. This situation is in contrast with that of aculeate Hymenoptera, of which 43 species were found on Anak Krakatau, a fauna little smaller than that (45–55) on the 3 other islands. The relative richness in aculeate species was explained by their preference for open sites and by the mutual-source-area effect of the component islands of the archipelago (Sk. Yamane, 1983).

5. *Diversity and disharmonity*

The tropical flora and fauna are typified by the extraordinary numbers of species of most taxa when compared with temperate flora and fauna (Ewusie, 1980). Therefore, one may expect many butterfly species to inhabit tropical forest. However, although the islands are certainly tropical, the total number of butterfly species on the Krakatau Islands was only 39, much fewer than the numbers in Java (583) and Sumatra (686) (Table 7), being only 6.69% and 5.68% of the numbers on Java and Sumatra, respectively. Of course, Java and Sumatra are much larger in size than the Krakataus,

Table 7. Number of butterfly species in different families on the Krakataus and ratio to the numbers on Java and Sumatra.

Family	Krakataus	Java	K/J (%)	Sumatra	K/S (%)
PAPILIONIDAE	3	34	8.82	46	6.52
PIERIDAE	5	48	10.42	46	10.87
DANAIDAE	4	35	11.43	34	11.76
SATYRIDAE	4	57	7.02	67	5.97
LIBYTHEIDAE	0	3	0	3	0
NYMPHALIDAE	4	115	3.48	147	2.72
LYCAENIDAE	16	155	10.32	180	8.89
HESPERIIDAE	3	136	2.21	163	1.84
TOTAL	39	583	6.69	686	5.68

but it is apparent that only a small portion of the butterfly fauna of Java and Sumatra has recolonized the Krakataus during the 100 years since the big eruption of 1883. Similar results were found for fruit fly species of the genus *Dacus* (YUKAWA, 1984) and for aculeate Hymenoptera (Sk. YAMANE, 1983).

Faunas of oceanic islands are known to be frequently disharmonious (CARLQUIST, 1974; KIMOTO, 1982), and remarkable examples of faunistic disharmony were found for some insect groups in the 1982 surveys. Sk. YAMANE (1983) pointed out the lack of swarm-founding social species in the Krakatau Aculeata and related this to the difficulty of a swarm completing a long trip over the sea. ABE (in preparing) found that the termite fauna of the Krakataus was characterized by the rarity of subterranean species and the abundance of wood dwellers and wood consumers which seemed to have more easily colonized the islands on drift wood. These examples of disharmony were thus referable chiefly to different means of dispersal of insect groups. For the butterfly fauna of the islands, disharmony was not so evident as a result of the 1982 surveys. K/J and K/S ratios were relatively low for Hesperiidae and Nymphalidae (Table 7). However, this is considered to be the result of vegetational succession (see below) rather than differential dispersal of butterfly families.

6. *Role of host plants in butterfly colonization*

As shown in Tables 2 & 4, the Krakataus lack many butterfly species which are thought to be commonly distributed in West Java. Table 8 lists the known host plant species or genera for the butterflies which were found in the 1982 surveys on Panaitan or at Carita but have never been collected on the Krakataus. It is remarkable that almost all these host plants and their close relatives are absent from the 1982 floral list of the Krakataus (TAGAWA & SUZUKI, unpublished) and from the collecting records from 1886 to 1972 (FLENLEY & RICHARDS, 1982). These plants have not yet colonized the Krakataus. Thus, the absence of host plants seems to be an important factor in preventing butterfly species from establishing themselves on the islands.

Since a large majority of butterfly species are oligophagous, a successful expansion of their distributional range strongly depends on the existence of host plants. In contrast, polyphagous insects can more easily invade new habitats as they have a greater chance of meeting a host plant, or may sometimes shift to other plants. Such an example was noted on Rakata Besar. The scale insect, *Crypticerya jacobsoni*, was in an outbreak situation (YUKAWA, 1984), infesting leaves and twigs of various plant species, particularly those of *Ficus* species which were not previously known to be hosts of the insect. Oligophagous butterflies, however, do not readily shift from their hosts on to newly encountered plants. The butterfly fauna is therefore determined to a large extent by the presence of particular species or genera of plants.

7. *Extinction and immigration*

Sixteen butterfly species which had previously been recorded on the Krakataus were not collected or observed during the 1982 surveys (Table 2). In order to assess the reliability of these absences, collecting records of previous floral surveys (FLENLEY & RICHARDS, 1982) and of the 1982 surveys (TAGAWA & SUZUKI, unpublished) were

Table 8. List of butterflies collected at Carita and on Panaitan Island in the 1982 surveys but not known from the Krakatau Islands, together with known host plants and collection records of the plants or their relatives on the Krakataus.

Family & Species of Butterflies	Species & Family of Host Plants	Coll. records of plants		
		1886–1979*	1982**	Note
PAPILIONIDAE				
□ *Graphium doson*	*Magnolia grandiflora* [Magnoliaceae]	none	none	
	Michelia alba [Magnoliaceae]	none	none	
	Michelia compressa [Magnoliaceae]	none	none	
	[Annonaceae]	none	none	
	[Lauraceae]	—	—	(1)
■ *Losaria coon*	*Apama tomentosa* [Aristolochiaceae]	none	none	
□ *Papilio helenus*	*Citrus* sp. [Rutaceae]	RB	none	(2)
	Evodia glauca [Rutaceae]	none	none	
	Phellodendron amurense [Rutaceae]	none	none	
	Toddalia asiatica [Rutaceae]	none	none	
	Zanthoxylum sp. [Rutaceae]	none	none	
□ *Papilio peranthus*	*Evodia glauca*? [Rutaceae]	none	none	
	Micromelum minutum [Rutaceae]	none	none	
PIERIDAE				
□ *Appias indra*	(Unknown)	—	—	
□ *Appias lyncida*	*Capparis zeylanica* [Capparidaceae]	none	none	
	Crataeva religiosa [Capparidaceae]	none	none	
□■ *Appias nero*	(Unknown)	—	—	
□ *Appias paulina*	*Capparis hyneana*? [Capparidaceae]	none	none	
	Drypetes australasica [Euphorbiaceae]	none	none	
	Putranjiva matsumurae [Euphorbiaceae]	none	none	
□ *Cepora iudith*	*Capparis* sp. [Capparidaceae]	none	none	
■ *Delias hyparete*	*Henslowia frutescens* [Santalaceae]	none	none	
	Loranthus chinensis [Loranthaceae]	none	none	
	Loranthus liquidam [Loranthaceae]	none	none	
	Loranthus pentandrus [Loranthaceae]	none	none	
	Dendropthoe pentandra [Loranthaceae]	none	none	
□ *Gandaca harina*	*Ventilago oblongifolia* [Rhamnaceae]	none	none	
□ *Pareronia valeria*	*Capparis hyneana* [Capparidaceae]	none	none	

Table 8. (*continued*)

Family & Species of Butterflies	Species & Family of Host Plants	Coll. records of plants		
		1886–1979*	1982**	Note
DANAIDAE				
□ *Euploea crameri*	*Cryptolepis panciflora* [Asclepiadaceae]	none	none	
	Ficus glomerata [Moraceae]	none	RB, S	(3)
	Ficus indica [Moraceae]	none	none	(3)
	Nerium oleander [Apocynaceae]	none	none	
■ *Euploea modesta*	(Unknown)	—	—	
■ *Euploea mulciber*	*Aristolochia* sp. [Aristolochiaceae]	RB	none	(4)
	Ficus benjaminea [Moraceae]	none	none	(3)
	Ficus formosana [Moraceae]	none	none	(3)
	Ficus retusa [Moraceae]	RB	none	(3)
	Ichnocarpus volubilis [Apocynaceae]	none	none	
	Nerium oleander [Apocynaceae]	none	none	
SATYRIDAE				
■ *Amathusia* sp.	▲ *Cocos* spp. [Palmae]	RB	ALL	(5)
	▲ *Nypa* spp. [Palmae]	none	none	
■ *Elymnias* sp.	▲ *Arenga* spp. [Palmae]	none	none	
	▲ *Cocos* spp. [Palmae]	RB	ALL	(5)
	▲ *Livistona* spp. [Palmae]	none	none	
	▲ *Nypa* spp. [Palmae]	none	none	
NYMPHALIDAE				
□ *Cethosia hypsea*	[Passifloraceae]	—	S	(6)
□ *Charaxes* sp.	(Unknown)	—	—	
□ *Euthalia* sp.	(Unknown)	—	—	
■ *Junonia atlites*	*Asteracantha longifolia* [Acanthaceae]	none	none	
	Barleria sp. [Acanthaceae]	none	none	
LYCAENIDAE				
□ *Jamides elpis*	(Unknown)	—	—	
□ *Jamides malaccanus*	(Unknown)	—	—	
□ *Miletus* sp.	▼ Aphids	—	—	
? □ *Nacaduba pactolus*	(Unknown)	—	—	

* Collection records of plant species on Rakata Besar from 1886 to 1972 based on FLENLEY & RICHARDS (1982).
** Collection records of plant species in 1982 based on TAGAWA & SUZUKI (unpublished) and TAGAWA (1983, personal communication).
■ Collected at Carita.
□ Collected on Panaitan Island.
▲ These are not host plants of particular species, but representative hosts of the genera *Amathusia* and *Elymnias*, respectively.
▼ Butterflies of the genus *Miletus* are known to feed on aphids, having a symbiotic relation to such ants as *Polyrachis dives* and *Dolichoderus bituberculatus*.
? Doubtful identification.
RB: Rakata Besar Island.
S: Sertung Island
ALL: Four islands including Rakata Besar, Rakata Kecil, Sertung and Anak Krakatau.
(1) Only one species of Lauraceae, *Cassytha filiformis* has been known to exist on the Krakataus since 1896/97, but it may not be a host plant of *G. doson*.
(2) *Citrus* sp. was collected from Rakata Besar on 2 occasions in 1919/20 and 1922.
(3) At least 15 species of the genus *Ficus* occur on the Krakataus.
(4) *Aristolochia tagala* existed on Rakata Besar from 1919 to 1934.
(5) *Cocos nucifera* was observed on Rakata Besar in 1896/97, and it was found on all 4 islands in 1982 in restricted areas.
(6) *Passiflora foetida* was found on Sertung in 1982, but it may not be a host plant of *C. hypsea*.

Table 9. List of butterflies previously collected on the Krakatau Islands but not found in the 1982 surveys, together with known host plants of the butterflies and collection records of the plants or their relatives on the Krakataus.

Family & Species of Butterflies	Species & Family of Host Plants	Coll. records of plants		
		1886–1979*	1982**	Note
DANAIDAE				
Danaus melanippus	*Gymnema* spp. [Asclepiadaceae]	none	none	
	Tylophola spp. [Asclepiadaceae]	RB	AK	(1)
SATYRIDAE				
Orsotriaena medus	*Imperata arundinacea* [Gramineae]	RB	ALL	(2)
	Oryza sativa [Gramineae]	none	none	
Ypthima philomela	▲ *Microstegium ciliatum* [Gramineae]	none	none	
	▲ *Pogonatherum critinum* [Gramineae]	RB	ALL	(3)
NYMPHALIDAE				
Cirrochroa tyche	(Unknown)	—	—	
Moduza procris	*Mussaenda frondosa* [Rubiaceae]	RB	RB	(4)
	Sarcocephalus missionis [Rubiaceae]	none	none	
	Setephagyne parvifolia [Rubiaceae]	none	none	
	Wendlandia exserta [Rubiaceae]	none	none	
	Wendlandia notonana [Rubiaceae]	none	none	
Phalanta phalantha	*Flacourtia* spp. [Flacourtiaceae]	none	none	
	Salix spp. [Salicaceae]	none	none	
LYCAENIDAE				
Catochrysops panormus	*Cajanus cajan* [Leguminosae]	none	none	
	Dolichos spp. [Leguminosae]	RB	none	(5)
	Phaseolus spp. [Leguminosae]	RB	none	(6)
Catopylops ancyra	(Unknown)	—	—	
Deudorix jarbas	(Unknown)	—	—	
Loxura atymnus	*Dioscorea* spp. [Dioscoreaceae]	RB	RB, S	(7)
	Smilax spp. [Liliaceae]	RB	RB, RK, S	(8)
HESPERIIDAE				
Notocrypta sp.	(Unknown)	—	—	
Pelopidas conjunctus	*Andropogon* spp. [Gramineae]	none	none	
	Bambusa spp. [Gramineae]	none	none	
	Saccharum officinarum [Gramineae]	RB	ALL	(9)
	Zea mays [Gramineae]	none	none	

Table 9. (*continued*)

Family & Species of Butterflies	Species & Family of Host Plants	Coll. records of plants		
		1886–1979*	1982**	Note
Pelopidas mathias	*Cymbopogon nardus* [Gramineae]	none	none	
	Imperata cylindrica [Gramineae]	RB	ALL	(2)
	Oryza sativa [Gramineae]	none	none	
	Saccharum officinarum [Gramineae]	RB	ALL	
Polytremis lubricans	*Imperata cylindrica* [Gramineae]	RB	ALL	
Tagiades sp.	(Unknown)	—	—	
Telicota augias	▲ *Calamus* spp. [Palmae]	RB	RB, S	(10)
	▲ *Cocos nucifera* [Palmae]	RB	RB, S, AK	(11)
	▲ *Imperata cylindrica* [Gramineae]	RB	ALL	(2)
	▲ *Oryza sativa* [Gramineae]	none	none	

* Collection records of plant species on Rakata Besar from 1886 to 1972 based on FLENLEY & RICHARDS (1982).
** Collection records of plant species in 1982 based on TAGAWA & SUZUKI (unpublished) and TAGAWA (1983, personal communication).
▲ These are not host plants of particular species but representative hosts of the butterfly genera concerned.
RB: Rakata Besar Island.
RK: Rakata Kecil Island.
S: Sertung Island.
AK: Anak Krakatau Island.
ALL: Four islands including Rakata Besar, Rakata Kecil, Sertung and Anak Krakatau.
(1) There are records of 3 species of *Tylophola* on Rakata Besar during the period from 1931 to 1979, but in the 1982 surveys only 1 species, *T. asthmatica* was observed in a restricted area of Anak Krakatau and it was not collected on Rakata Besar.
(2) *Imperata cylindrica* was recorded on Rakata Besar from 1896/97 to 1979, but in the 1982 surveys it was found only in restricted areas on Anak Krakatau.
(3) *Pogonatherum paniceum* has been recorded from Rakata Besar since 1896/97, but it is now rare on the Krakataus.
(4) *Mussaenda frondosa* has been recorded from Rakata Besar since 1922.
(5) *Dolichos* sp. was collected from Rakata Besar on only 1 occasion in 1979.
(6) *Phaseolus adenanthus* was recorded on Rakata Besar from 1924 to 1931/32, but it has not been found on the Krakataus since.
(7) *Dioscorea oppositifolia* was collected on Rakata Besar in 1928/29. Another unidentified species of *Dioscorea* was found on Rakata Besar in 1979 and in 1982, and on Sertung in 1982.
(8) *Smilax zeylanica* has been recorded from Rakata Besar since 1922, and it was also found in 1982 on Rakata Besar and Rakata Kecil.
(9) *Saccharum spontaneum* has existed on Rakata Besar since 1896/97; its existence there was reconfirmed and it was recorded on the 3 other islands in 1982. However, except on Anak Krakatau, it is now very rare.
(10) *Calamus unifarius* and *Calamus viminalis* were collected on Rakata Besar in 1979, but not in 1982. An unidentified species of *Calamus* was collected on Sertung in the 1982 surveys.
(11) *Cocos nucifera* has been recorded from Rakata Besar since 1896/97 and it was found on all 4 islands in 1982 in restricted areas.

examined for their known host plants or relatives there (Table 9).

A single specimen of a nymphalid, *Phalanta phalantha* was observed by Jacobson in May 1908 on Rakata Kecil and was not seen again since (DAMMERMAN, 1948). *P. phalantha* may not have established itself on the Krakataus as its host plant has not yet colonized the islands. The absence from the 1982 collection of *Danaus melanippus*, *Moduza procris* and *Loxura atymnus* may be due to the incompleteness of the survey because their host plants still exist commonly on the islands (TAGAWA & SUZUKI, unpublished).

In contrast, it is highly probable that some species whose larvae feed on Gramineae or Palmae have become extinct on the Krakataus. In the 1982 surveys Gramineae and Palmae were certainly found on all four islands, but their distribution was very limited, having been largely replaced by other forest trees, particularly on the islands other than Anak Krakatau (TAGAWA *et al.*, in press). In addition, the number of Gramineae species has apparently been reduced (FLENLEY & RICHARDS, 1982). As pointed out by MACARTHUR & WILSON (1963), a species is more likely to become extinct when its population density is reduced under conditions of limitation of habitat and food resources. Therefore, the above-mentioned changes in vegetation may have promoted the extinction of some satyrids and hesperiids which are associated with Gramineae or Palmae. A lycaenid, *Catochrysops panormus* appears to be a genuine extinction due to the succession of vegetation (Table 9). Thus, at least 7 species are considered to have become extinct on the Krakataus since the 1930s as a result of the extinction or decline of their hosts.

In contrast to the above examples of extinction, 14 butterfly species which had never been found on the Krakataus were collected or observed in 1982 on the islands for the first time. They are listed in Table 10, together with their known host plants, except for 3 species whose hosts have not yet been noted. According to the collecting records of plant species, the known hosts of *Graphium agamemnon* and *Zizina otis* have not yet colonized the Krakataus and that of *Pelopidas agna* has become extinct on the islands. The occurrence of the first 2 species may be considered to be temporary as has been noted for *Phalantha phalantha*, for no alternative hosts are known. The third species, *P. agna* may possibly have other hosts of Gramineae as well as *Paspalum conjugatum*.

The remaining species are mostly lycaenids, being associated with forest trees or their undergrowth, particularly with species of Leguminosae. Most species, except 2 hesperiids on Gramineae, may be regarded as *K*-selected species. These spcies are considered to have colonized the islands after the development of forest, later than such *r*-selected species as grassland inhabitants.

8. *Colonization curve*

Table 3 shows the number of butterfly species which were collected or observed on the Krakataus during the present and previous surveys. The total species number on the Krakataus markedly increased from 6 in 1908 to 32 in 1919–1922, and then slightly decreased to 29 in 1934 (Fig. 3). According to the 1982 surveys the species number has increased from 29 in 1928–1934 to 39. The change was largely the result of a

Table 10. List of butterflies collected in 1982 for the first time on the Krakatau Islands, together with known host plants and collection records of the plants or their relatives on the Krakataus.

Family & Species of Butterflies	Species & Family of Host plants	Coll. records of plants		
		1886–1979*	1982**	Note
PAPILIONIDAE				
Graphium agamemnon	*Annona discolor* [Annonaceae]	none	none	
	Annona reticulata [Annonaceae]	none	none	
	Annona squamosa [Annonaceae]	none	none	
	Michelia alba [Magnoliaceae]	none	none	
	Michelia figo [Magnoliaceae]	none	none	
	Michelia fuscata [Magnoliaceae]	none	none	
PIERIDAE				
Eurema alitha	*Pithecellobium dulce* [Leguminosae]	RB	RB	(1)
DANAIDAE				
Euploea sp.	(Unknown)	—	—	
LYCAENIDAE				
Allotinus ferderi	(Unknown)	—	—	
Jamides aratus	(Unknown)	—	—	
Megisba malaya	*Allophylus timorensis* [Sapindaceae]	none	S	(2)
	Mallotus japonicus [Euphorbiaceae]	none	none	
	Mallotus paniculatus [Euphorbiaceae]	none	none	
	Mallotus philippensis [Euphorbiaceae]	none	none	
Miletus symethus	(Aphids)	—	—	
Petrelaea dana	*Terminalia catappa* [Combretaceae]	RB	ALL	(3)
Prosotas dubiosa *Prosotas lutea*	▲ *Entada parvifolia* [Leguminosae] ▲ *Entada phaseoloides* [Leguminosae]	RB	RB	(4)
Zizina otis	*Alysicarpus vaginalis* [Leguminosae]	none	none	
	Mimosa pudica [Leguminosae]	none	none	
Zizula hylax	*Lantana* spp. [Vernenaceae]	RB	RB, RK, S	(5)
	Nelsonia campestris [Acanthaceae]	none	none	
	Vicia spp. [Leguminosae]	none	none	

Table 10. (*continued*)

Family & Species of Butterflies	Species & Family of Host Plants	Coll. records of plants		
		1886–1979*	1982**	Note
HESPERIIDAE				
? *Borbo cinnara*	*Paspalum conjugatum* [Gramineae]	RB	none	(6)
	Saccharum sinense [Gramineae]	RB	ALL	(7)
? *Pelopidas agna*	*Paspalum conjugatum* [Gramineae]	RB	none	(6)

* Collection records of plant species on Rakata Besar from 1886 to 1972 based on FLENLEY & RICHARDS (1982).

** Collection records of plant species in 1982 based on TAGAWA & SUZUKI (unpublished) and TAGAWA (1983, personal communication).

▲ These are representative host plants of the genus *Prosotas*.

RB: Rakata Besar Island.

RK: Rakata Kecil Island.

S: Sertung Island.

ALL: Four islands including Rakata Besar, Rakata Kecil, Sertung and Anak Krakatau.

? Doubtful identification.

(1) *Pithecellobium umbellata* has been known from Rakata Besar since 1905/6.

(2) *Allophylus cobbe* was first found in 1982 on Sertung.

(3) *Terminalia catappa* has been known from the Krakataus since 1896.

(4) *Entada phaseoloides* has been known from Rakata Besar since 1924.

(5) *Lantana camara* has been known from Rakata Besar since 1905/6, and it is now commonly seen on islands other than Anak Krakatau.

(6) *Paspalum conjugatum* was collected on Rakata Besar in 1928/29 and 1931/32, but it has not been found on the Krakataus since.

(7) *Saccharum spontaneum* has existed on Rakata Besar since 1896/97; its existence there was reconfirmed and it was recorded on the 3 other islands in 1982. It is now very rare on islands other than Anak Krakatau.

prominent increase of lycaenids.

PRESTON (1962) and MACARTHUR & WILSON (1963) independently suggested that on islands there might be a balance of immigration by extinction so that the diversity of at least some biotas could be understood as an equilibrium (MACARTHUR & WILSON, 1967). A dynamic equilibrium is reached when immigration and extinction rates are equal; namely colonization rate falls to zero. The immigration and extinction rates of butterfly species on the Krakataus could not be calculated because of insufficient collecting data and irregular census intervals. However, the colonization curve for total species (Fig. 3) indicates that the species number is still increasing on the islands.

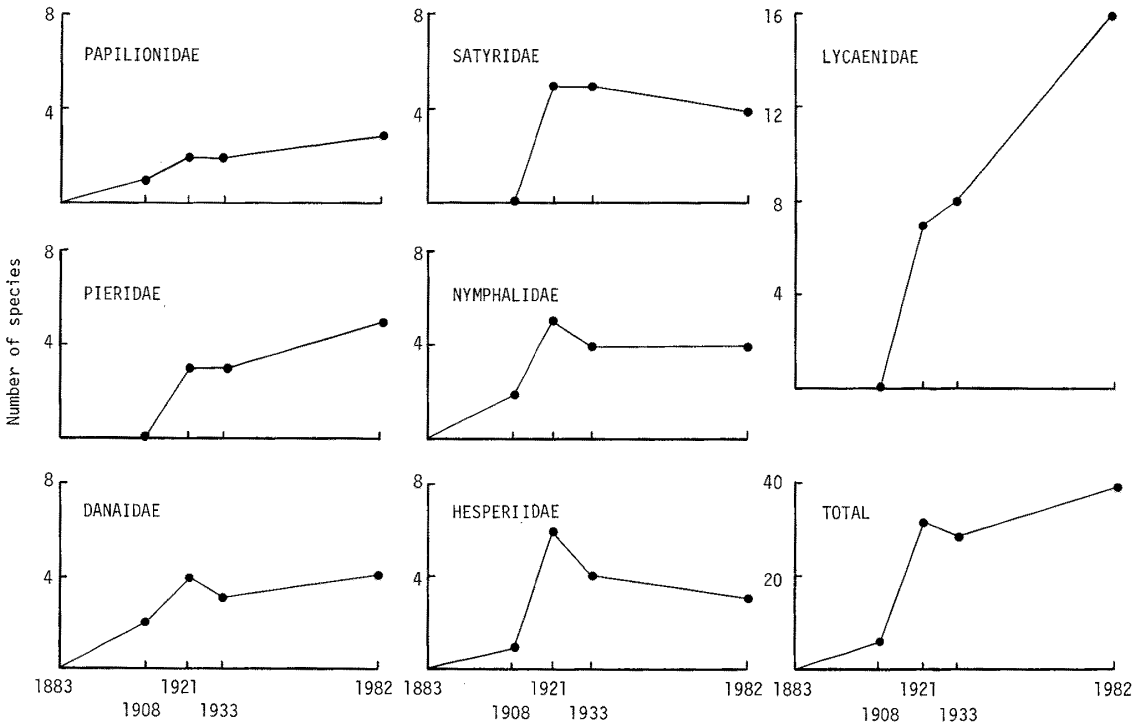

Fig. 3. Colonization curves for butterfly species on the Krakatau Islands.

According to TAGAWA *et al.* (in press), at least seven different stages are recognizable during the course of vegetational succession from 1883 to the present status. Based chiefly on his previous data (TAGAWA, 1964) on the vegetational succession in the temperate regions, TAGAWA (1983, personal communication) considers that on the Krakataus there will be many more stages on the way to climax forest and that each stage will last at least 10 years. WHITTAKER *et al.* (1984) also predict that, 'in the absence of major disturbance by humans, volcanicity, or other factors, the size of the flora of Rakata will continue to increase rather slowly by the addition of "primary" forest species, with the gradual decline (and sometimes loss) of some "secondary" forest species. A progression to the status of "primary rain forest" (="tropical seasonal forest" in the sense of TAGAWA *et al.*, in press), with its implied diversity of species is clearly a very long way off'.

In accordance with the vegetational succession the species number of butterflies will neccessarily change in the future since recolonization by such oligophagous plant-

feeders as butterflies largely depends on the presence or absence of their host plants as has already been discussed. If it is considered that each stage of the succession has the capacity to carry a certain number of species, a kind of "pseudo-equilibrium" would be reached during the period of a stage, which may be 10 or more years. The carrying capacity of a given stage not always be larger than that of the preceding one; this will depend on the particular plant species which constitute the stages. The colonization curve would, therefore, become stepped rather than smooth, involving occasional decreases in species number (Fig. 4). Such a curve is somewhat different from that for polyphagous plant-feeders or predacious organisms. Sk. YAMANE (1983) presented colonization curves for aculeate Hymenoptera collected on the Krakataus. These curves would be expected to be much smoother and to reach equilibrium earlier than that for butterflies, because the recolonization by aculeate Hymenoptera is considered to be indirectly influenced by the vegetational succession.

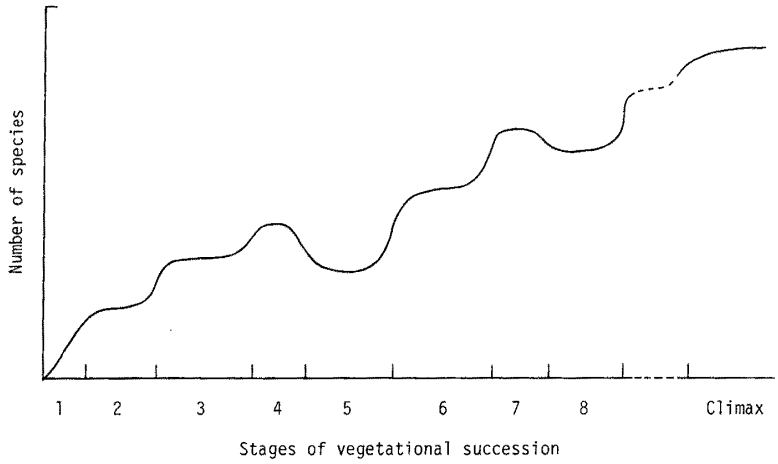

Fig. 4. Schematic representation of a possible colonization curve for oligophagous plant-feeding insects.

It is desirable to continue monitoring the ecological succession on the Krakatau Islands because they are providing an irreplaceable example of a long-running natural experiment on the tropical ecosystem. The author supports the suggestion of Sk. YAMANE (1983) that intesnive surveys be performed every 10 years from now in order to obtain further data for the analysis of the recolonization process.

Acknowledgements

The author would like to express his hearty thanks to the Indonesian Institute of Sciences, and to Prof. H. TAGAWA (Kagoshima University, Leader of the two Japanese expedition teams) for giving him an opportunity to study the organisms on the islands. The author received kind help in identifying the butterflies, and valuable suggestions and information concerning host plants and distribution range of some butterflies from the following entomologists in Kyushu University: Prof. T. SAIGUSA (Papilionidae & Lycaenidae), Asocc. Prof. A. NAKANISHI (Nymphalidae), Dr. H. SHIMA

(Danaidae & Satyridae), Mr. O. YATA (Pieridae & Hesperiidae) and Mr. N. KÔDA (Nymphalidae). The draft was critically read through by Dr. I. W. B. THORNTON (La Trobe Univ., Australia), Prof. T. SAIGUSA, Mr. O. YATA (Kyushu Univ.) and Mr. Sk. YAMANE (Kagoshima Univ.), and some butterflies were collected by Mr. Sk. YAMANE and Dr. E. SUZUKI (Kagoshima Univ.), to whom the author is deeply indebted. The vegetational information was provided through the courtesy of the two plant ecologists in the teams, Prof. H. TAGAWA and Dr. E. SUZUKI (Kagoshima Univ.). Gratitude is also expressed to Mr. H. FUKUDA (Kagoshima Prefectural Museum) for his kindness in providing the author with valuable references, to Mr. K. TAKENAKA (NHK) for his information on the butterflies which he observed in June 1983 on Rakata Besar and Anak Krakatau, to Miss Y. IKESHIMA (Kagoshima Univ.) for her assistance in preparing the draft, and to Dr. T. ABE (Kyoto Univ.) and Dr. T. IWAMOTO (Miyazaki Univ.) for their help in various ways during the field survey on the islands.

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摘　　要

インドネシアのクラカタウ諸島におけるチョウ相の地理生態学（湯川淳一）

インドネシアのジャワとスマトラの間のスンダ海峡にあるクラカタウ諸島の動植物は，1883年の大噴火で死滅したと言われており，その後の動植物の再移住に伴う生態遷移の過程は地理生態学者らの注目の的になっている．筆者は，爆発後100年目の昆虫相を調査するために，1982年にこれらの島々と周辺地域（パナイタン島とジャワ西海岸のチャリタ村）を訪れる機会を得た．

他の昆虫に比較してチョウは同定が容易で，しばしば，亜種の区別まで可能である．また，寄主植物や分布に関する知見も多い．さらに，どの調査でもチョウの採集や目撃の記録は数多く報告されている．したがって，寄主植物そのものの分布や採集記録が同時に備わっていれば，チョウは地理生態学上，恰好の研究材料となり得る．幸いにもクラカタウ諸島の植物相の遷移に関しては，これまで比較的充実した調査・研究がなされており，チョウのような食植性昆虫の再移住を考察する上で，きわめて有益な情報が用意されている．

クラカタウ諸島では39種，パナイタン島では29種，チャリタ村では18種のチョウを採集した．クラカタウ諸島とパナイタン島で採集したチョウの大部分のものはジャワ亜種に属しており，これらの島々へは，スマトラよりもむしろジャワから移住した種の方が多いことが明らかとなった．クラカタウ諸島4島全体での39という種類数は，ジャワの583種の6.69%，スマトラの686種の5.68%に当り，この100年間でまだほんの一部のチョウしか再移住していないことを示している．ジャワでの種数に対する割合を科別で比較してみると，セセリチョウ科が2.21%で最も低く，シロチョウ科とマダラチョウ科，シジミチョウ科が10.32～11.43%と高かった．島の生物相では，しばしば，不調和性が見られるが，クラカタウの蝶相ではあまり顕著ではなかった．

クラカタウ諸島は4つの小さな島からなっており，その内の1つ，子クラカタウ島は1927年から1930年にかけての海底火山の活動によって形成された新しい島である．この島は面積も小さく（280ha），植物は約50種，しかも，それらの生育地が限られているために，チョウも僅か8種しか確認できなかった．これに対し，面積が大きく，地形も複雑で，植生も比較的豊富な大ラカタ島（1,152ha）やセルツング島（784ha）ではより多くの種類が採集された．

ジャワ西海岸のチャリタ村やパナイタン島で，きわめて普通に見られる何種かのチョウがクラカタウ諸島でまったく採集できなかった．これらのチョウの寄主植物を調べてみると，いずれも，植物そのものがクラカタウ諸島に移住していないことが判明した．また，ヤコブソンやダンメルマンらがクラカタウ諸島の昆虫相を調べた1908年から1932年にかけて，島に生息していたいくつかのチョウが1982年の調査で発見されなかった．これらの大部分のチョウの寄主植物も，かつては島に繁茂していたにもかかわらず，現在では絶滅したか，あるいは，生育場所が限られているということがわかった．とりわけ，イネ科やヤシ科を寄主としていたチョウは島から消えていったものが多い．これとは反対に，これまでクラカタウ島で採集されたことのないチョウが14種も新しく記録された．とくに，シジミチョウ科が多かった．草原などオープンランドに生息する，いわゆる*r*-淘汰を受けた種にかわって，*K*-淘汰を受けた種が遅れて移住してきたものと考えられた．

このように，植生の遷移に伴って種の入替りが起こりつつ，クラカタウ諸島のチョウの種類数は，1908年の6種から1919～1922年の32種へ，そして，1928～1934年の29種から1982年の39種へと変化してきた．マッカーサーとウイルソンは島に移住してくる生物の移入率と移住した生物の絶滅率が等しくなる時点で，島における種類数は平衡に達すると述べている。今回示したクラカタウ諸島へのチョウの移住曲線の増加傾向からも明らかなように，チョウの種類数は爆発後100年を経過した現在も平衡状態に達しているとは考えられない．

島を調査した植物生態学者らは，いわゆる熱帯季節林と呼ばれる極相林に達するのに，なお多くの年月を要し，様々な植生段階を経過すると予測している．また，1つの植生段階は10年以上も継続すると言われている．そうだとすれば，寄主植物の遷移に大きく依存しているチョウ相は今後も変化し続け，種類数も増加していくに違いない．しかし，その時々の植生段階の優占種やその他の構成樹種が合わせもつ一定の容量によって最高種数が決定されるため，その植生段階が続く間，種類数はいわゆる偽平衡に達するであろう．したがって，移住曲線はなめらかに増加するのではなく，植生の遷移に応じて段階的に変化していくものと考えられる．

クラカタウ諸島は長期に亘る生態遷移を研究する上で掛け替えのない天然の大実験場と言える．これまで提唱された地理生態学に関する様々な理論を検証するためにも，また，再移住の過程を分析するに足る多くのデーターを得るためにも，今後の定期的な調査の必要性を強調しておきたい．